

Hypothesizing novel mating behaviours in the squaretail grouper based on direct behavioural observations

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Abstract

Historically unfished, high-density spawning aggregations are vanishingly uncommon. Behavioural observations from such aggregations are rare, and may be sometimes novel and unexpected. Given the weight of evidence required to document spawning aggregations, how can we best report rare and unusual behavioural variations in spawning populations? Based on two years of in-water observations of a high-density spawning aggregation of the squaretail grouper in the Lakshadweep Archipelago, we described a previously unreported male alternative reproductive tactic (ART) and an inverse size assortment with large males courting several small females that shoaled mid-water (<https://doi.org/10.1186/s12898-017-0120-5>). In critiquing our manuscript, it has been suggested that our observations, methodologies and interpretation are inadequate, flawed, and do not fit within currently accepted theory (<https://doi.org/10.1186/s12898-018-0206-8>). While offering a detailed counter of the main methodological and theoretical criticisms we question how best to document and interpret novel behaviours in poorly known systems. Reporting novelty itself can hardly be the basis of criticism. Our report relied on direct in-water observations, conducted at peak densities over two spawning years. The critique ignores this, choosing instead to focus on a supplementary video which was not the basis of our conclusions. Like other researchers working on this species, we did not directly observe mating, but report courtship as a well-established proxy used across mating systems studies. Apart from these methodological concerns, the authors suggest that there is no theoretic-

cal support for our observations. However, sexual selection theory provides well-established frameworks showing that, at very high mating densities, a variety of tactics can emerge, that often vary considerably between populations and locations. In our original paper, we use this broader theory of sexual selection together with detailed behavioural data to propose plausible evolutionary explanations that bear testing in these novel, high-density systems. We agree with the authors that novel observations should be scrutinised carefully as they can challenge our current understanding of the range of behaviours populations display and serve as a springboard for theoretical advancement. Given their rarity, these observations should be evaluated against the rigour of their documentation and the transparency of their reporting. In this context, we hope our carefully documented observations serve as a useful addition to the fascinating and complex natural history of species like the squaretail grouper.

Introduction

Theoretically grounded natural history is the foundation on which behavioural ecology rests. Observations in the real world demonstrate the range of responses species can show under a spectrum of contexts and conditions. Behaviours at extremes of this spectrum are particularly insightful since they serve as vital tests of theory. Given how important these observations are, it is only right that they are subject to greater intellectual scrutiny than mere confirmations of the norm. However, field observations at these extremes are typically rare and often limited to anecdotal accounts that are difficult to verify. It is therefore critical, in the few instances where circumstances make it possible, that studies follow standardly accepted protocol and are transparent in their reporting. These are the standard burdens of proof required for any observational study, and the scientific community should ask no less – and no more of these observations to include them in the canon of theoretical and observed species behaviours. When done right, observations at the extreme can challenge and advance our understanding of behavioural theory, even when they may require further observations and tests to confirm them.

In a manuscript published in the journal *BMC Ecology* (Karkarey et al. 2017), we reported a rare set of observations of mating behaviours of the squaretail grouper (*Plectropomus areolatus*) at a spawning aggregation in the Lakshadweep Archipelago before the population was fished. The densities of groupers we recorded at the aggregation were among the highest recorded anywhere, and our detailed observations over two years confirmed that, at these high densities, this species shows two distinct courtship tactics – a pair courtship (also recorded elsewhere across the range of this species. E.g. Johannes 1988; Pet et al. 2005) and a previously unreported school courtship tactic. Based on in-water observations we proposed that the school courtship likely leads to a unique ‘school spawning tactic’ where larger males spawn with several smaller females in mid-water schools. Our findings contributed to efforts by the local community and government agencies to protect the aggregation from fishing – a protection that continues to this day. In a recent critique of our paper, Erisman et al. (2018) suggest that our reported results were based on a single “fake” observation of single-male multi-female spawn without empirical or theoretical basis, that we likely did not observe actual

spawning, and that the inverse-size assortment we report is based on invalid methods and an inaccurate interpretation of theory. These allegations are troubling since we have clearly set out the theoretical framework of sexual selection and mating systems in our paper, used standard ecological and behavioural methodologies, and carefully discussed our inferences together with the limitations of our study and future directions to test the explanations we propose. More fundamentally, the critique raises questions about the weight of evidence required to legitimately document unusual behaviours that may occur only at the extremes of population density, given their rarity. While we respond here to the principal objections raised in the critique, we encourage readers to read through our original manuscript, Karkarey et al. (2017), where we have reported our observations with considerable detail and clarity.

Documenting inverse size assortment and alternative reproductive tactics in a high density spawning aggregation

Our paper documented mating behaviours of the squaretail grouper at a natural and extreme end of the density spectrum that had not been previously addressed in the literature. The squaretail grouper has more usually been observed at spawning aggregations exposed to years of fishing and human disturbance. We monitored reproductive behaviour for over two years in the absence of fishing activities, using carefully designed and well-established ecological and behavioural methodologies. At peak densities, we recorded an average of 72.08 ± 27.46 fish per 1000 m^3 ($200\text{m}^2 \times 5\text{m}$ depth) across the spawning site. Densities were more than 4 times higher on the slope of the spawning site, where we documented the alternative school spawning tactic (Karkarey et al. 2017). Our paper explores how these observations might add to our understanding of the maintenance of alternative reproductive tactics (ARTs). Our paper lays out the limitations of this observational study and makes clear that it is not a confirmatory test of hypotheses for the evolution of the alternative reproductive behaviours we report. Rather, we use the broader theory of sexual selection together with detailed behavioural data to propose plausible evolutionary explanations for the interesting behavioural variation we report. The two main processes we draw upon are:

1. the influence of density on the expression of alternative reproductive tactics and
2. the role of female behaviour and choice in influencing male mating tactics.

Both these are common processes that have been tested across the animal kingdom.

Here, we respond to the allegations made by Erisman et al. (2018), describing in detail why we think our methodology, inferences and explanations are robust and contextually relevant to studying natural history and animal behaviour. Their principal concerns with our study are broadly methodological (false observation of spawning event, not sampling at peak spawning periods, and using invalid measures of courtship

rates in spawning fish) and theoretical (no support for single male-multi female mating in broadcast spawning fish). We address each of these points in the sequence in which they raise them.

1. False observations of spawning events involving a single male with multiple females

We observed courtship patterns at the Bitra aggregation for two years using in-water observations by three of us (RK, RA and AZ). All the conclusions of our original manuscript are based on direct observations. Much of the critique of our works focuses on a forensic analysis of a supplementary video we submitted along with the manuscript. However, this gives the video more importance than it deserves. The video was captured by a remote underwater camera, when we were NOT in the water and at no point in our paper do we present the video as conclusive evidence but merely as supporting what we observed in situ. The two incidents of ‘school spawning’ have been described as a sequence of events, culminating in gamete release in our manuscript (Karkarey et al. 2017). These were observed directly by us in the water, at a distance of less than 5m from the female school. These observations of natural history have been recorded in the text of our original paper in as clear and precise a way as possible (Karkarey et al. 2017, pages 5, 6). The video merely adds to our confidence of the prevalence of ‘school courtship’ and potential spawning behaviour.

The work of Johannes (1978, 1988), Johannes et al. (1999) and Pet et al. (2005), which Erisman et al. (2018) have mentioned, have documented reproductive behaviours in groupers in much the same way, i.e. relying on direct in-water observations or on many of the same proxies that we have used (ie. swollen bellies, spawning colouration, male behaviours, etc.). As we explain in the paper, because the aggregation was seasonally protected, more invasive and destructive techniques were not available to us. More generally, in diverse taxa, behavioural work is commonly conducted using direct observations, especially for rare behaviours (see for instance, Bro-Jørgensen 2002; Young et al. 2009; Surbeck et al. 2011). It is therefore puzzling that the authors have taken the video as our primary (or only) evidence, when the original article makes it clear that it is the direct observations that are the primary evidence (a misreading of our words that is repeated time and again throughout their commentary).

2. No empirical evidence of single male – multiple female spawning in *P. areolatus*, groupers, or any other coral reef fish

Erisman et al. (2018) provide descriptions of the behaviour of female shoals and squaretail groupers as observed in other regions and critique the behavioural observations in our paper based on them not having been reported earlier. It is difficult to know how to respond to this critique, given that the precise purpose of our manuscript was to report observations we believed were unique and noteworthy. While

these behaviours were certainly brief and anomalous to what is known, we emphasize that they were observed multiple times across two years, under specific density conditions in this population. Even while doubting our observations of unique mating behaviour, Erisman et al. (2018) insist that there is nothing unique about ARTs in the *P. areolatus*. They provide a detailed account of other ARTs reported for this species by past researchers (Johannes 1978, 1988; Johannes et al. 1999; Pet et al. 2005; Rhodes et al. 2014) from different regions. We agree with the authors that the schooling behaviour of female squaretail grouper schools is not novel and has been reported previously (Johannes et al. 1999). We acknowledge this in our paper too, but emphasize the differences as we observed them in the Lakshadweep aggregation. In particular, we describe that female schools were larger than reported previously (>150 females), size-specific, and unlike the descriptions provided by Johannes et al. (1999), the schools formed a cohesive unit – ie. females did not break free from this school to follow males into their territories after male courtship forays (Karkarey et al. 2017, page 5). In addition, the Palauan example of the multiple male-single female courtship interaction that Johannes et al. (1999) recorded, had a very high male:female sex ratio unlike the Lakshadweep aggregation. However, in the same paper, Johannes et al. (1999) also describe that “*In a Solomon Islands spawning aggregation, where female P. areolatus outnumbered males, Johannes (1989) observed that the males were typically attended by several females, and he saw no harassment of females by males*”. This description resembles our observations of single male – multiple female courtship associations on the slope, where population sex ratios were highly skewed towards females. Together, these observations only strengthen the growing understanding that, at high densities, species may employ a wide suite of reproductive tactics that are lost as densities decline. There exists a substantial behavioural ecology literature showing that mating tactics can vary between closely related species, between populations of the same species, and even within a population (Emlen and Oring 1977; Apollonio 1989; Clutton-Brock and Vincent 1991; Lott 1991; Brockmann 2001; Taborsky 2008). A wide variety of factors, including population density, operational sex ratios, habitat, and environmental contexts can lead to differential expression of mating and other behaviours (Clutton-Brock and Vincent 1991; Brockmann 2001; Tomkins and Brown 2004; Thirgood et al. 1991; Davies 1991). Several lekking ungulates show cross-population variation in mating behaviour, with only a few populations showing lekking (Clutton-Brock and Vincent 1991; Thirgood et al. 1991). Furthermore, lekking may disappear from a population when density declines, for example due to hunting (Clutton-Brock and Vincent 1991).

The authors of the critique call into question our observations and our broader understanding of grouper mating systems, although we have specifically acknowledged the diversity of mating strategies of groupers with relevant citations (Karkarey et al. 2017, Page 2). As we clearly explain in our paper, the behaviour we report may be associated with particularly high density aggregations, which as we report, is extremely rare given the strong fishing pressures experienced by these groupers globally (Sadovy de Mitcheson et al. 2013). It is therefore not surprising that such behaviours have not

been observed previously (including by Erisman et al. 2018). All the more reason, then, to carefully report these behaviours when they are observed, since they greatly inform our understanding of high-density mating tactics.

3. No theoretical support for single male – multiple female spawning in broadcast spawning fishes

A major point of contention is how population density specifically affects grouper mating systems. Erisman et al. (2018) state that mate monopolization by territorial males is negatively correlated with population density in groupers, supported by empirical evidence and their own literature review (Erisman et al. 2009). They expect that at lower densities, pair spawning and territorial tactics exist and with increasing density, group spawning is seen. We have no argument with this at the usual density ranges earlier reported for this species. However, as we are at pains to report in our manuscript, at densities much higher than previously reported, other tactics might arise, when both mate competition and mating stakes are high enough to select for an alternative (and more costly) way of gaining mates. The tactics we identify are the conventional pair spawning one (which, in our system, appears to be a low-cost, low-benefit tactic) and the high-cost, high-benefit tactic of ‘school spawning’. We describe this in elaborate detail in our paper (Karkarey et al. 2017). In this tactic, large males hold territories in a dense aggregation that provide access to large female schools. But courtship and mating takes place external to these territories. Males temporarily leave these territories to make forays into the schools, which is highly costly, as males risk losing their territories, but at the same time, may benefit from gaining seven times higher potential mating opportunities. Thus, like Erisman et al. (2018), we also argue that at high densities, conventional mate monopolisation through pair spawning is increasingly difficult. The sole point of contention appears to be that Erisman et al. (2018) expect only group spawning under high density while we report a different school spawning tactic, that we suggest may be a variation of, or precursor to, group spawning (Karkarey et al. 2017, page 9).

Variation in mating tactics between populations of the same species is hardly unusual. Density (or potential mates) can interact with environmental factors to affect mating tactics in complex ways (Emlen and Oring 1977; Kokko and Rankin 2006). We would once again like to reiterate that the densities we reported in this aggregation are higher than those reported previously in squaretail grouper aggregations, so it is not surprising that the behaviour we report has not been previously discussed – and precisely why we believed it was important to report. Refuting a tactic we report based on that it has not been reported before is not a valid criticism.

Erisman et al. (2018) state that we report puzzling female behaviours without placing them in the context of theory. Particularly they ask “*Why would multiple females choose to risk their eggs on a single male’s sperm release when numerous other males are present?*”, alleging that we claim “egg competition”. This bears some explanation.

Firstly, there is a rich body of work showing that male and female mating tactics are more variable than previous thought. Males and females may make mating decisions that are not initially “intuitive” but are adaptive when studied over individual lifetimes. For example, paternity studies have shown that in bighorn sheep (*Ovis canadensis*), subordinate, younger males following a ‘low-benefit’ harassment tactic gain almost as much paternity as dominant males following a mate-guarding tactic (Hogg and Forbes 1997). Similarly, in many taxa, females engage in covert matings with subordinate, younger or satellite (often presumed to be of lower quality) males (e.g., Lank et al. 2002; Ortega et al. 2003).

Secondly, multiple females mating with a single male is not puzzling but seen commonly as in the case of leks. In lek mating systems, females are commonly choosy about mates, exhibit strong mate choice and mating success is commonly highly skewed towards a small percentage of males. In addition, even in such extreme polygynous systems, associations between multiple females and a single male, and female-female competition for individual males on leks have been reported (Bro-Jørgensen 2003). Depending on male quality or site quality or direct benefits gained from males, females may show unanimous mate choice which may result in multiple females associating with the same individual males. At no point do we claim ‘egg competition’ but we assume the authors of the critique refer to the situation of multiple females associating with a single male in a short period of time – discussed in the literature in the context of sperm limitation. In our paper we propose that females show condition dependence, with smaller females potentially trading off current reproductive success with growth for potentially higher reproductive success in the future. In the literature, this trade-off between growth and current reproductive success is seen when females run the risk of sperm limitation (Berglund 1991). These provide plausible explanations for the question posed by the critics: why females would “choose to risk their eggs on a single male’s sperm release when numerous other males are present”. We have acknowledged in our manuscript that these explanations remain to be tested by other, more direct methodologies in this aggregation. The possibilities described above are discussed at length in our paper, and we are puzzled that the authors appear to have missed them while claiming that we do not provide plausible explanations from within the classical and current theory of sexual selection, life history theory and ARTs. However, even had we not been able to think of plausible explanations from current theory for our observations, it would not be a reason to not report them.

4. Insufficient evidence that observations were made during the actual spawning period

The authors suggest that we did not sample during spawning periods. However, as we described in detail in the paper (Karkarey et al. 2017, Page 3), we carefully established spawning seasonality and diel specificity of this aggregation by conducting extensive in-water surveys across months and lunar phases. We supplemented our direct inwater surveys with the help of local informants who monitored the site in our absence.

To reiterate, we found that groupers arrive two days before the new moon, reached their highest densities on new moon day and then dropped in density by 80% the day after new moon, and by 98% by the third day after the new moon. In the absence of histological means to assess spawning time, we triangulated the spawning time based on the dramatic drop in densities after new moon day and the absence of highly gravid females at the aggregation site after new moon days. In addition to this, from our focal behavioural observations we found that males spent upto 50% more time in intra-sexual aggression on the evenings of new moon days compared to days and periods prior to and after the new moon. Taken together, our in-water observations gave us enough confidence that we were sampling as close to the spawning period as possible (ie. afternoons of new moon days).

5. No evidence of “inverse size-assortment” due to invalid methods used to estimate courtship rates

The criticism that we used invalid methods to estimate courtship rates has also been carefully addressed in our original paper. We have clearly described that we do not measure courtship rates, but in fact measure ‘association rates’ as a proxy for ‘potential mating opportunities’ (Karkarey et al. 2017, page 4). However, considering that this is a fish spawning aggregation, and that sampling was conducted close to spawning period (on peak aggregation days), it is reasonable to assume that male-female interactions were courtship, especially when the sequence of behaviours that we observed and describe in the paper has been documented as courtship behaviours in other studies of this species (Pet et al. 2005).

Male fitness is ideally measured over an individual’s life time and using genetic methods to determine paternity (Clutton-Brock and Sheldon 2010). However, such assessments of male fitness are rare for wild populations. Studies of diverse taxa and both in the field and in the lab typically use proxies of fitness, e.g., number of offspring, number of matings, number of females a male associates with (Alberts et al. 2003; Brommer et al. 2005; Alonso et al. 2010; Jiguet and Bretagnolle 2014). The last measure, the number of females a male associates with, is a commonly used proxy for male reproductive success in wild populations (Alberts et al. 2003; Alonso et al. 2010; Jiguet and Bretagnolle 2006, 2014; Lappin and Husak 2005). Even in controlled experiments in the lab, associations between males and females are taken to represent mating decisions – for example, experiments on female preference for male phenotype in many taxa use the time spent by a female close to a male (or model) as indicative of her preference of mate (Godin et al. 2005; Griggio et al. 2011; Heuschele et al. 2009). We have clearly stated in our paper (Karkarey et al. 2017) that we use association rates as a proxy for potential mating opportunities. We explain why mating rates are a challenge to measure (like in many other taxa) and also explain why we believe our index serves as a reasonable proxy for potential mating opportunities.

Conclusions

We wholeheartedly agree with Erisman et al. 2018 of the need for rigour and care in understanding mating behaviour. Our interpretation of the ecology of mating systems and the arguments we make are actually very similar to the ones Erisman et al. (2018) have themselves laid out in their criticism. Our suggestion that high density can favour the appearance and maintenance of alternative reproductive tactics is supported by theory (Kokko and Rankin 2006) and empirical work (Clutton-Brock et al. 1997; Kokko and Rankin 2006). Furthermore, the argument we make that differences in female spatial distribution and preferences can maintain multiple male mating tactics is also supported in the literature (Clutton-Brock 2007; Stockley and Bro-Jørgensen 2011). The broad arguments made by us and Erisman et al. (2018) (that male and female mating tactics may be density dependent) actually match, differing largely in the specifics of the behaviour displayed under high density that we report versus that expected by the critics. Most of the criticisms appear to stem from the authors misreading our original paper. We would encourage the authors and all readers to once again closely read our methodology to resolve any remaining confusion. We thank the authors for their patient criticisms and we encourage them in turn to engage with the wider theory of mate choice and sexual selection with open mindedness.

Writing in the 1970s, Paul Feyerabend (1975) was convinced that unsavoury brawling was unavoidable in science, but he was even more insistent that a proliferation of observations and theories is required to overcome the ‘chauvinism of science that resists alternatives to the status quo’. As our detailed observations show, species like the squaretail grouper have a broader suite of reproductive tactics than previously imagined. It does not challenge what we know about the species, it instead adds to it.

Author contributions

RK and RA conceived and designed the experiments, performed the experiments, analyzed the data, authored and reviewed drafts of the paper and approved the final draft. AZ performed the experiments, authored or reviewed drafts of the paper. KI conceived and designed the experiments, analyzed the data and authored or reviewed drafts of the final paper. RK and RA 60%, KI 20%, AZ 20%.

Authors	Contribution	ACI
RK and RA	0.60	3.000
KI	0.20	0.500
AZ	0.20	0.500

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